CHAPTER III

MORPHOLOGICAL AND PHYSIOLOGICAL RESPONSES OF SORGHUM (*Sorghum bicolor* L. Moench) TO WATERLOGGING

Introduction

One of the considered influencing factors for the recent world food crisis is renewable energy from agriculture products. It has been criticized as a humiliation by diverting crops from food to bio-fuel feedstock and resources competition, water or land, leaving 800 million people in hunger or undernourishment worldwide (FAO, 2008). Second-generation biofuel technologies, based on lignocellulosic feedstock, have been proposed to reduce this competition (FAO, 2008). Native or external plant species with fast growing rate, high net energy yield and low input requirements, particularly capable of being grown on marginal lands, are being intensively researched (Schmer *et al.*, 2008). One potential energy crop is *Sorghum bicolor* (L.) (Reddy *et al.*, 2005; Corredor *et al.*, 2008). In addition, land use intensification such as sequential cropping, intercropping or crop rotation of energy crop with food crop is one of the solutions (Mal´ezieux *et al.*, 2009). However, in the tropical regions, most of the crops grown during the summer-rainy season frequently suffer intermittent or long-term waterlogging or flooding due to excess irrigation, storms, poor soil drainage or overflowing of the rivers. If this energy crop is incorporated into the paddy fields, a massive occupied in tropical and sub-tropical areas, waterlogging has a particularly heavy effect on the crop, since repeated puddling breaks capillary pores, reduces void ratio, destroys soil aggregates and disperses fine clay particles as well as when a rising water table and rainfall intensity combine with low evapotranspiration (Polthanee, 1997).

This paper was accepted for publication in Asian Journal of Plant Sciences, *Volume. 9: 183-193.*

These lead energy crops to be more commonly subjected to waterlogging or flooding. Therefore, information about sorghum responses to waterlogging is essential.

Growth and physiological processes are detrimentally affected by waterlogging. Waterlogging decreases the leaf elongation rate and leaf area of plants (Orchard and Jessop 1984; Dias-Filho and Carvalho, 2000; Malik *et al.*, 2001, 2002; Henshaw *et al.*, 2007), and consequently reduces plant height and ultimately suppresses root and shoot production (Haung *et al.*, 1994).

Stomata closure, reduction of transpiration and inhibition of photosynthesis are common responses that can occur in hours or days, depending on the tolerance to waterlogging of each species and cultivar. When waterlogging is prolonged, waterlogging-intolerant plants drastically reduce their physiological activities and are often killed in a short time, whereas, in waterlogging-tolerant plants the same parameters could even be enhanced or have less effect due to the ability of roots to acclimate to waterlogging, such as by the ability to produce adventitious roots and aerenchyma formation (Dias-Filho and Caryalho, 2000; Pang *et al.*, 2004; Striker *et al.*, 2005; Irving *et al.*, 2007; Li *et al.*, 2007; Mollard *et al.*, 2008)

Growth related to physiological response under waterlogging stress in sorghum has not yet been elucidated. Understanding how plants respond to waterlogging is important in determining their potential for use in habitat prone to this stress.

Therefore, the objectives of this study were to: (1) investigate morpho- and physiological changes in sorghum in response to waterlogging; and (2) compare the waterlogging tolerance of four sorghum cultivars.

Materials and Methods

Plant culture and treatments

The experiment was conducted at the Moorbank Botanical Garden at the University of Newcastle (UK) School of Biology, from February to April 2008. Seeds of sweet sorghum (*Sorghum bicolor* L. Moench) cv. Wray, Keller, Bailey and multipurpose sorghum (*Sorghum bicolor* L. Moench) cv. Suphanburi 1 (SP1)

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(Supanburi Field Crop Research Centre, Thailand) were planted in pots with 450 g of 6:2:1 (peat: sand: potting base) culture. The potting base contained 7.5% nitrogen, 3.6% phosphorus, and 5.2% potassium. Prior to planting, pots were watered to field capacity (FC), and then three to five sweet sorghum seeds were drilled into each pot at 2 cm depth. At the two-leaf stage, plants were thinned to one plant per pot. Water was applied daily to FC by weighing random selected pots on a balance. Waterlogging was applied at the vegetative stage (five fully expanded leaves) of each cultivar (Vanderlip and Reeves, 1972). Pots containing growing plants were placed in a larger pot, and water was applied daily to the soil surface for 20 days. Control pots were free-draining and were watered daily. To avoid unexpected effects from the outer pots on plant growth, control pots were also placed in the empty larger pots (Irving *et al.*, 2007). Pots were arranged in environmentally controlled conditions, where the temperature was 13/26 °C (min/max), and with a 14 h photoperiod with the additional light of 400-watt high-pressure sodium bulbs (Pang *et al.*, 2004). The pots were arranged in a 2 x 4 factorial randomized complete block design with four replications of waterlogging treatment and two replications of control treatment (Irving *et al.*, 2007).

Plant growth measurements

During the waterlogging period, the length of the youngest expanding leaf was measured daily using a ruler to determine youngest leaf expansion rate (YLER) (Dias-Filho and Caryalho, 2000). The length was measured from soil surface to the top of new emerged leaf. Plant height, senescent leaf number and leaf area were recorded at four-day intervals. A non-destructive leaf area measurement method was adopted, according to Wright (1981). At the end of the waterlogging treatment, 20 days after waterlogging (DAW), plants were destructively harvested. The length of the longest nodal root and nodal root number were recorded (McFarlane *et al.*, 2003). Root, leaf and culm were dried at 80 °C for 48 h, and then the plant's dry weight was recorded. Shoot: root biomass ratio was calculated (Ye *et al.*, 2003).

Photosynthetic measurements

Photosynthetic rate (A, $\mu mol\ m^{-2}\ s^{-1}$), stomatal conductance (gs, $mol\ m^{-2}\ s^{-1}$) and transpiration rate (E, $mmol\ m^{-2}\ s^{-1}$) were collected with a LCi portable photosynthesis system (ADC Bioscientific Ltd., Hoddesdon, UK). Measurements were taken from the youngest fully expanded leaf of each plant (Pang *et al.*, 2004). These measurements were made from 11.00 to 13.00 hrs, with the following specifications/adjustments: leaf surface area, 6.25 cm^2; ambient CO_2 concentration, 385μmol mol^{-1}; and temperature of leaf chamber varying from 32.37 °C to 34.33 °C. Photosynthetically active radiation (PAR), provided by 400-watt high-pressure sodium bulbs, was set at the leaf surface to 700 μmol m^{-2} s^{-1} (Ashraf and Rehman, 1999). Measurements were conducted at 0, 4, 8, 12, 16 and 20 days after waterlogging (DAW).

Statistical analysis

The data for all physiological and growth parameters were subjected to analysis of variance using Statistix 8 software (Analytical software, 2003). The mean values were compared using the least significant difference test.

Results

Shoot growth response to waterlogging

Waterlogging significantly reduced plant height and the adverse effects were more pronounced when duration of waterlogging increased. At 4 days after waterlogging (DAW), cv. Wray and Bailey could maintain plant height to control plants but cv. Keller and SP1 showed a 10% reduction from their respective controls. However after 8 DAW onwards, a higher height reduction with longer waterlogging duration was found. At 20 DAW, height of Keller was reduced to 30% (Fig.1c), Bailey was reduced to 33% (Fig.1e) and SP1 was reduced to 35% (Fig. 1g) as compared to the control. In contrast, cv. Wray after 12 DAW onwards had height reduction maintained at 18-20% lower than the control (Fig. 1a).

Reduction in plant height was consistent with the decrease in youngest leaf expansion rate (YLER). Waterlogging significantly reduced YLER of all cultivars, being lowest in Cv. Wray (Fig.1b), while progressively decreasing in cv. Keller (Fig. 1d), Bailey (Fig. 1f) and being highest in SP1 (Fig. 1h).

LA was significantly affected by waterlogging, with advancing reduced when waterlogging duration was extended. Different responses were noted among studied cultivars. Cv. Wray could maintain LA similar to control plants at 4 DAW and began to reduce at 8 DAW while the other three cultivars started to decline at 4 DAW onwards. After 12 DAW to 20 DAW LA reductions in cv. Wray were between 56%-65% (Fig. 2a). However, in cv. Keller it increased from 43% at 12 DAW to 62% at 20 DAW (Fig. 2c), or 34% to 72% in cv. Bailey (Fig. 2c) and the highest persistence was in cv. SP1 (74% to 80%) (Fig. 2d).

The reduction in LA was concurrent with the acceleration in leaf senescence. Waterlogging significantly increased the senescent leaf number of all studied cultivars in terms of the onset and change during the waterlogging period. Senescent leaf no. gradually increased at 8 DAW in cv. Wray and Bailey and reached a maximum at 16 DAW and 20 DAW, respectively (Fig. 2e and g). However, a sharp rise to maximum was noted in cv. Keller at 8 DAW onwards (Fig. 2f). Nevertheless, the development of senescent leaf no. was delayed in cv. SP1, started at 12 DAW (Fig. 2h).

Shoot biomass was severely affected by 20 days of waterlogging with 71% compared to the control. This was due to the decrease in culm dry weight (DW) (68%) and leaf DW (72%). All cultivars had a similar response and no interaction between water regimes and cultivars was found (Table 1). However, under waterlogging conditions, Cv. Wray showed relatively higher shoot DW, followed by cv. Keller and Bailey and lowest in cv. SP1.

Root growth

Waterlogging significantly reduced nodal root (NR) number plant^{-1}, longest root length (LRL), and consequent root DW, compared to the control plants. NR number plant^{-1}, LRL and root DW were reduced to 24%, 28% and 71% compared to the control plants, respectively (Table 1).

Cultivar variation responses were found in all root growth parameters. Interestingly, compensation between NR number and LRL was observed. The lowest NR number was found in cv. Wray (16 plant^{-1}), but it had the longest LRL (399 mm plant^{-1}) (Table 1). Interactions between water regimes and cultivars on NR number and LRL were also noted. Cv. Bailey had the highest NR number (30 plant^{-1}), whereas the lowest was found in waterlogged Wray (13 plant^{-1}) (Fig. 3a). LRL was highest in the control (502.75 mm plant^{-1}) and lowest in waterlogged cv. Wray (272 mm plant^{-1}) (Fig. 3b). However, no interaction was noted in terms of root DW.

Shoot/root ratio

Shoot /root ratio (S/R) was significantly higher in plants under waterlogged conditions than in freely drained pots (Table 1). A statistically different interaction was found. Further analysis showed that waterlogged SP1 had the lowest S/R, while the highest was found in waterlogged Wray (Fig. 3c).

Physiological response to waterlogging

Leaf gas-exchange characteristics of all sorghum cultivars were significantly affected by waterlogging varying in cultivars studied. The intensification was more pronounced with longer duration of waterlogging. Photosynthetic rate (A) of sweet sorghum, cv. Wray, Keller and Bailey, started to decline at 4 DAW, with 29%, 58% and 31%, respectively, compared to their controls but unchanged in cv. SP1. The degree of the reduction was maintained to 8 DAW and accelerated to 57% at 12 DAW and was lowest at 20 DAW 78% in cv. Wray (Fig. 4a). In cv. Keller, the adverse effect was alleviated at 8 DAW (35%) and 12 DAW (40%). However, prolonged waterlogging duration reduced A of Keller to 65%-70% (Fig. 4b). In cv. Bailey, the response was found similar to cv. Wray but with higher suppression at 77% reduction at 20 DAW (Fig. 4c). In contrast to sweet sorghum, waterlogging reduced A of forage sorghum, cv. SP1 only at 8 DAW (11%). And starting from 12 DAW onwards, A was increased over the control, giving 56% higher than controls at 20 DAW (Fig. 4d).

Stomatal conductance (Fig. 4e-h) and transpiration rate (data not shown) followed a similar pattern to that observed for photosynthesis.

Discussion

Four sorghum genotypes in this experiment responded to waterlogging similarly in terms of shoot and root biomass accumulations but study of root growth, dry matter partition and leaf gas exchange parameter showed drastic differences in their responses.

The significant shoot growth reduction (71%) was due to the restricted development of plant height (30%), LA (69%) and thus decreased dry matter accumulation in leaf (72%) and culm (68%). This finding is in agreement with the findings in maize (Zaidi *et al.*, 2003, 2004), wheat (Malik *et al.*, 2001), barley (Pang *et al.*, 2004), buckwheat (Matsuura *et al.*, 2005), ryegrass (McFarlane *et al.*, 2003), soybean (Henshaw *et al.*, 2007) and mungbean (Ahmed *et al.*, 2002).

The pronounced reduction in shoot growth in this study is described by its high susceptibility to waterlogging at vegetative stage of *S. bicolor* due to its lack of nodal root development as compared to other growth stages (Our experiment). In this study, even though plant height and leaf area were reduced, waterlogging did not cause a significant reduction to biomass of shoot and root among cultivars. This indicates that these cultivars are tolerant to waterlogging conditions. Our previous experiment demonstrated that continuous flooding sweet sorghum from 30 DAE (8-10 leaf stage) until harvest only reduced shoot biomass and stalk yield to 20% and 22%, respectively. However, to investigate up to what extent they can withstand continuous flooding at the early vegetative stage further experiment is required. No significant difference in shoot biomass but significant reduction in shoot length and LA in response to waterlogging is also reported in *Hibicus esculentus* (Ashraf and Arfan, 2005).

The present study showed that even with a lack of differences in total biomass accumulation between aerobic and anaerobic treatment, significant differences in biomass allocation patterns was found. This is consistent with the response to waterlogging of *Sporobolus virginicus* (L.) Kunth (Naidoo and Mundree, 1993).

Results of this experiment indicate that the biomass partitioned to root in cv. SP1 is utilized for the initiation of new nodal roots. However, there was a competition for assimilates between shoot and root growth, resulting in slow shoot growth. This is in contrast to cv. Wray, where more assimilates was allocated to support shoot growth. This supports the result of Ye *et al.* (2003), who indicated that a shift of biomass from root to shoot is an adaptation to prolonged waterlogging in the higher waterlogging tolerance mangrove species (*Kandelia candel*). The significant reduction in photosynthate allocation to belowground parts, while maintaining aboveground biomass accumulation is reported as an effective metabolic strategy to reduce belowground oxygen demand and to increase the potential of shoots to transport oxygen to root of *Sporobolus virginicus* (L.) Kunth (Niadoo and Mundree, 1993). Therefore, it could possibly be concluded that in sorghum biomass portioning to shoot is an acclimation response to long-term waterlogging at early growth stage.

Leaf elongation rate has been proposed as an early detection mechanism for relative flood tolerance in grass species such as *Brachiaria spp.* Dias-Filho and Carvalho (2000) and Dias-filho (2002) or maize Lizaso and Ritchie (1997). Our results show that cv. Wray has the ability to extend the youngest leaf and produce new leaves, indicating that this cultivar is relatively tolerant to waterlogging. However in cv. SP-1, YLER was sharply decreased at day 2 after applying waterlogging, and continued decreasing over time, indicating that cv. SP-1 is relatively intolerant to waterlogging. Cv. Keller (as well as cv. Bailey) has the ability to maintain YLER for at least five days after waterlogging and then gradually decrease. This may imply that these two cultivars are quite tolerant to short-term waterlogging. Coincident increasing in senescent leaf number of cv. Wray, Keller and Bailey during waterlogging implies that these new growths may be supported by the remobilization of nutrients from older parts. This finding is consistent with the response of lucerne to waterlogging (Irving *et al*., 2007).

Adventitious root or nodal root development has been reported as the key root acclimation to waterlogging or flooding (Pardales *et al*., 1991; McDonald *et al*., 2002; Pang *et al*., 2004; Polthanee *et al*., 2008; Changdee *et al*., 2009). However, Van Noordwijk and Brouwer (1993) suggested that more developed roots may be less able to adapt morphologically (such as development of aerenchyma) under stress conditions. A relatively extensive aerenchyma spaces noted in cv. Wray than cv. SP1 in previous experiment may support the previous concept.

Zaidi *et al*. (2003) indicated that an early adventitious rooting is one of the crucial morphological traits of maize to tolerate excess soil moisture stress. This is in agreement with our results, indicating that sweet sorghum possesses this root acclimation trait, while multipurpose sorghum does not. In addition, our results showed that in cv. Wray even with lowest nodal root number, it had significant highest individual root length. This may presumably be a partial compensation to conserve root area for water and nutrient uptake during waterlogging. It was also observed that during waterlogging, the nodal root of cv. Wray was located near the soil surface indicating that this cultivar possesses root acclimation to reach atmospheric oxygen. This supports the results of Niadoo and Mundree (1993), who indicated that waterlogging tolerant *Sporobolus virginicus* (L.) possesses morphological responses to waterlogging such as fewer, but taller and more mature culm with greater aerenchyma spaces and production of aboveground adventitious roots close to the aerobic zone.

Thus, the present experiment indicates that the early nodal root development, the ability to maintain root surface area for water and nutrient uptake, and to develop aerenchyma spaces in existing roots and nodal root development near the soil surface during the susceptible stage are root morphological acclimations to survive and concurrently sustain plant growth under prolonged waterlogging conditions.

The decreased photosynthetic rate, as well as transpiration rate, in our experiment may be partially regulated by stomatal closure, due to a high positive correlation between stomatal conductance and photosynthesis under both control and waterlogged conditions (Fig. 5). Other findings (Huang *et al.*, 1994; Malik *et al.*, 2001; Asharf, 2003; Striker *et al.*, 2005) have also shown that stomatal conductance is the major factor effecting photosynthesis under waterlogging conditions in plants. Nevertheless, in this study, a positive significant correlation coefficient between photosynthetic rate and nodal root number of cv. SP1 (Fig. 6) may indicate that the newly-developed NRs of this cultivar are efficient functioning during the stress.

In addition, factors regulating photosynthesis in plants grown in waterlogged soil may be reduced CO_2 transfer conductance from sub-stomatal cavities to the site of carboxylation, or activity of photosynthetic enzymes at the carboxylation point. A marked increase in sub-stomatal CO_2 (Ci) noted in waterlogged cv. Wray, Keller and Bailey in relation to control plants, compared with comparative levels between waterlogged and freely drained plant in cv. SP1 (data not shown), may confirm that point. This is consistent with the finding of Malik *et al.* (2001), who reported that this may be responsible for decreased photosynthesis in waterlogged wheat. However, to draw such relationship in sorghum in response to waterlogging, a further experiment is needed.

Nevertheless, the observed response of photosynthesis to CO_2 indicates that a relevant limitation to photosynthesis of *S. bicolor* under waterlogging conditions may be caused by a reduced capacity of RuBisCo for CO_2 fixation, not translocation of CO_2 such as occurs in drought stressed sweet sorghum (Massacci *et al.*, 1996). Reduction of RuBisCO is closely related to total soluble protein content (Irving *et al.*, 2007) and is logically related to total leaf nitrogen content. The concurrent higher SPAD chlorophyll meter reading (SCMR) and photosynthetic rate (A) in cv. SP1, as well as a significant decrease in SCMR and A of cv. Wray, Keller and Bailey, throughout the experiment (data not shown), possibly implies that the leaf photosynthetic rate in waterlogged sorghum is partly regulated by chlorophyll.

However, in sweet sorghum, particular cv. Wray, it is likely that the growth did not relate to chlorophyll. This is consistent with the finding in Blue panicgrass response to waterlogging (Asharf, 2003). This may be due to the remobilization of nitrogen from older plant parts to support shoot growth during waterlogging causing a reduction in photosynthetic rate.

Under waterlogging or flooding conditions, a positive relation between photosynthetic capacity and growth has been reported in Blue panicgrass (*Panicum antidotale* Retz.) (Asharf, 2003), barley (Pang *et al.*, 2004), *Paspalum dilatatum* (Mollard *et al.*, 2008), forage grass (*Brachiria brizantha*) (Dias-filho, 2002) or forage legume (*Lotus spp.*) (Striker *et al.*, 2005) due to the development of nodal roots or adventitious roots, which form extensive aerenchyma spaces which create a relatively low-resistance internal pathway and by enhancing mass flow transport of oxygen, carbon dioxide and ethylene between plant parts above water and submerged tissues (Jackson and Colmer, 2005).

This is in contrast to our findings. The present study showed that under waterlogging conditions cv. SP1 produces nodal roots similar to control plants and increased photosynthetic rate higher than the control at the end of the experiment. However, its height, LA, leaf DW and shoot DW had highest decrease. In contrast to cv. Wray, waterlogging significantly reduced nodal root number and photosynthetic rate. However, its height, youngest leaf expansion rate (YLER), LA and shoot biomass was less affected than cv. SP1. This indicates that there is no relationship between growth and photosynthetic capacity in sorghum under waterlogging conditions. This supports the results of Ashraf and Arfan (2005), who found that under waterlogging *Hibiscus esculentus* decreases photosynthetic rate but not its shoot biomass or *Triticum aestivum* under salt stress (Hawkins and Lewis, 1993). The concomitant reduction in shoot biomass and unaffected leaf photosynthetic rate is found in *Sporobolus virginicus* (L.) Kunth in response to the combination effects of waterlogging and salt stress (Naidoo and Mundree, 1993), which is consistent to the response of forage sorghum, cv. SP1, in this experiment.

Nevertheless, in comparison to wheat response to severe waterlogging (Malik *et al.*, 2001), photosynthesis is reduced to 82% compared with the control at 5 d after waterlogging. Our results indicate that sorghum has higher waterlogging tolerance than wheat since it took 20 d to suppress photosynthesis to a similar value (average 73% as compared to the control plants).

Significantly higher plant height, or the ability to extend the youngest leaf expansion rate per day, results in relatively higher shoot biomass during waterlogging in cv. Wray, and it can thus be concluded that cv. Wray may be the most waterlogging tolerant from an agronomic point of view, the maintenance of relatively high yield (Setter and Waters, 2003). Cv. Keller and Bailey are intermediate and cv. SP1 is sensitive to waterlogging. This indicates that sweet sorghum; especially cv. Wray has the potential to grow on waterlogging prone areas, whereas forage sorghum is more preferable on upland areas.

In cv. SP1, leaf photosynthetic rate was less affected by short-term waterlogging and during the long-term waterlogging duration leaf photosynthetic rate as well as transpiration rate and stomatal conductance increased over the control. It can thus be concluded that cv. SP1 is the most waterlogging tolerant from a physiological point of view, survival or maintenance of high growth rate under waterlogging, relative to non-waterlogged conditions (Setter and Waters, 2003). Cv. SP1 may be the most valuable cultivar for use in further breeding programs. At the same time, from an agronomic point of view, cv. Wray may be the most suitable for immediate use by agronomists. Therefore, it can be seen that physiological measurements can help in assessing highly physiology tolerant cultivars, which only a high-yield basis assessment may simply discard.

In conclusion, cultivar, maintaining the higher shoot growth, was not associated with the ability to develop higher nodal root and retain or least affect leaf photosynthetic rate. But it is related to biomass partitioning to shoot during long- term flooding, early nodal root development, accompanied with the ability to conserve root surface area for water and nutrient uptake as well as the ability to remobilize nutrients from older parts to support shoot growth such as cv. Wray. In contrast, keeping high photosynthetic rate by partitioning biomass to develop new roots was at the expense of shoot such as cv. SP1. Nevertheless, to comprehend the physiological response of this cultivar, further study is needed.

Acknowledgements

This research was financially supported by the Royal Golden Jubilee program of the Thailand Research Fund (grant no. PHD/0108/2547). The authors acknowledge the kind assistance of Brian Brown, technical manager from the School of Agriculture, Food and Rural Development and Moorbank Botanical Garden, School of Biology, University of Newcastle, UK, for providing equipment and facilities during the conduction of the experiment.

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Table 1 Effects of 20 days of waterlogging on aboveground and belowground growths of 4 sweet sorghum cultivars.

Treatments	Aboveground			Belowground			S/R
	Leaf DW (gplant^{-1})	Culm DW (gplant^{-1})	Shoot DW (gplant^{-1})	NR no. (plant^{-1})	LRL (mmplant^{-1})	Root DW (gplant^{1})	
Water regimes (W)							
Control	3.52 a	1.75 a	5.27 a	23.88 a	398.19 a	1.69 a	3.17 b
Waterlogged	0.99 b	0.56 b	1.55 b	18.06 b	286.94 b	0.49 b	3.56 a
Cultivars (C)							
Wray	2.24	1.22	3.46	16.00 b	399.00 a	1.00 b	4.02 a
Keller	2.41	1.22	3.63	18.13 b	335.00 b	1.05 b	3.53 a
Bailey	2.03	1.12	3.15	24.00 a	308.50 b	0.89 b	3.63 a
SP-1	2.34	1.07	3.40	25.75 a	327.50 b	1.41 a	2.27 b
Significance							
W	0.39**	0.17**	0.52**	3.21**	37.49**	0.14**	0.36**
C	0.40ns	0.17ns	0.54ns	4.53**	53.03**	0.20**	0.52**
W x C	0.57ns	0.24ns	0.77ns	4.71*	75.00**	0.21ns	0.73**

*,** Significant at $P \leq 0.05$ or 0.01 respectively and ns; not significantly different at 0.05 of probability

Values followed by the same letter in the same column are not significantly different at 0.05 and 0.01 probability.

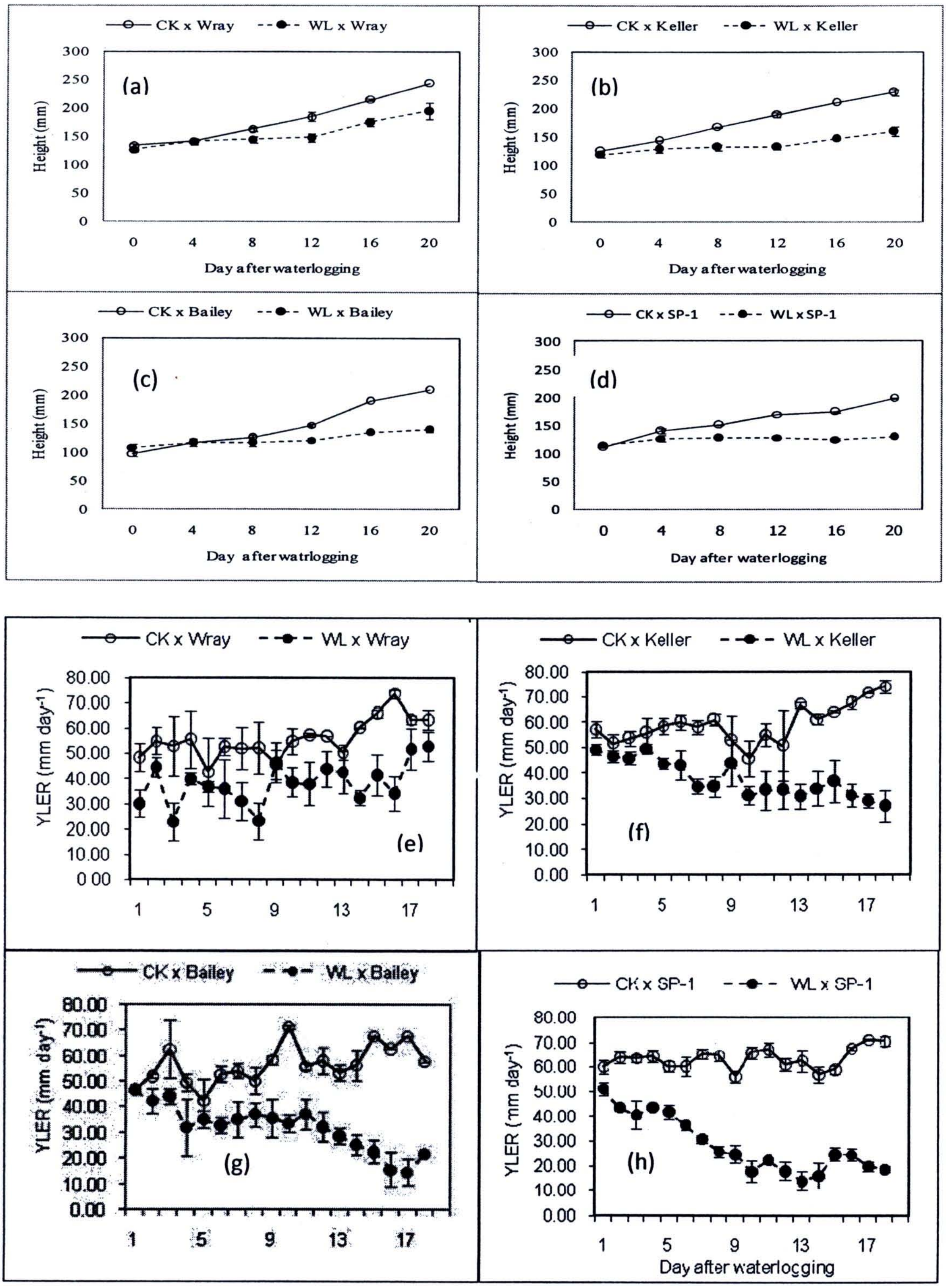

Figure 1 Effect of waterlogging on plant height (a, b, c and d) and youngest leaf expansion rate (YLER) (e, f, g and h) of 4 sorghum cultivars. Solid lines and open symbols represent control plants, broken lines and closed symbols represent waterlogged plants. Error bars represent standard errors.

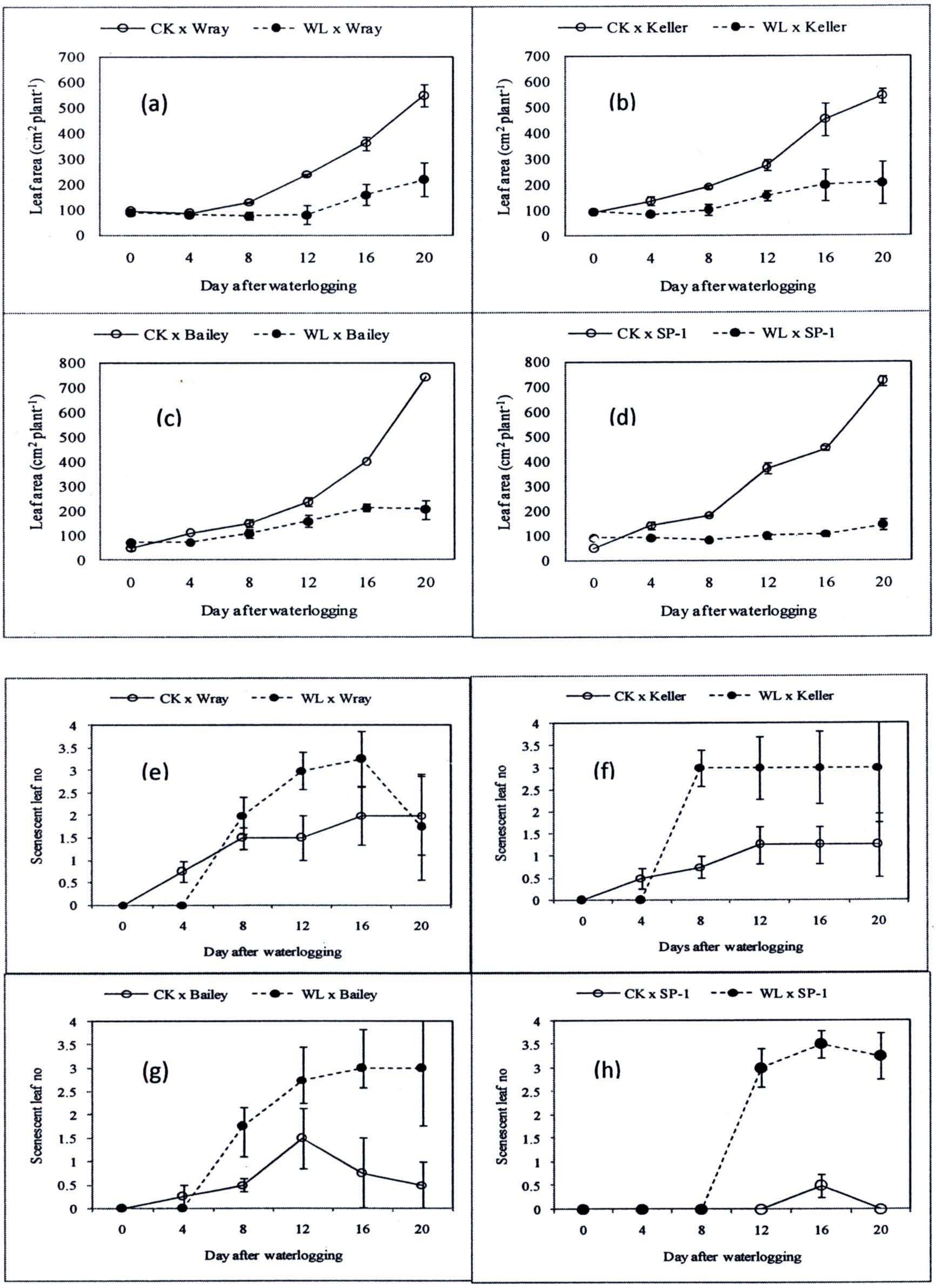

Figure 2 Effect of waterlogging on leaf area, LA, (a, b, c and d) and leaf senescent number (e, f, g and h) of 4 sorghum cultivars. Solid lines and open symbols represent control plants, broken lines and closed symbols represent waterlogged plants. Error bars represent standard errors.

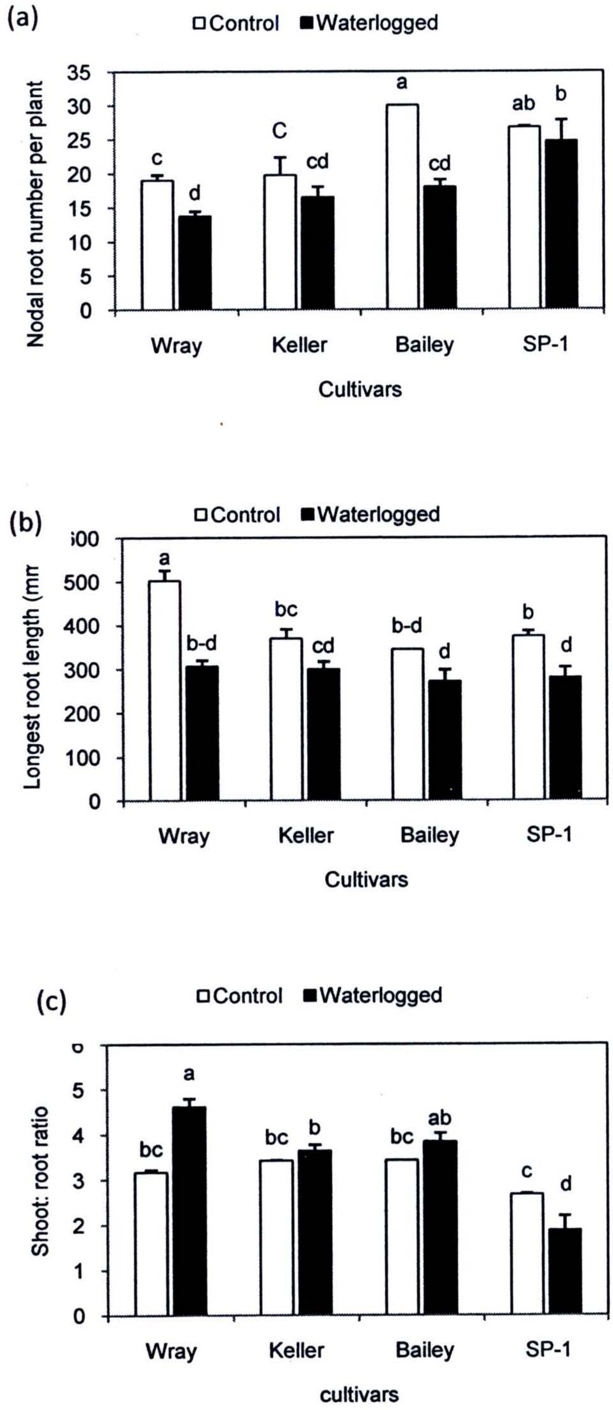

Figure 3 Effects of 20 days of waterlogging on nodal root number per plant (a), longest root length (b) and shoot/root ratio (c) of 4 sorghum cultivars. Values followed by the same letter in each growth stage are not significant different at 0.05 and 0.01 probability. Error bars represent standard error.

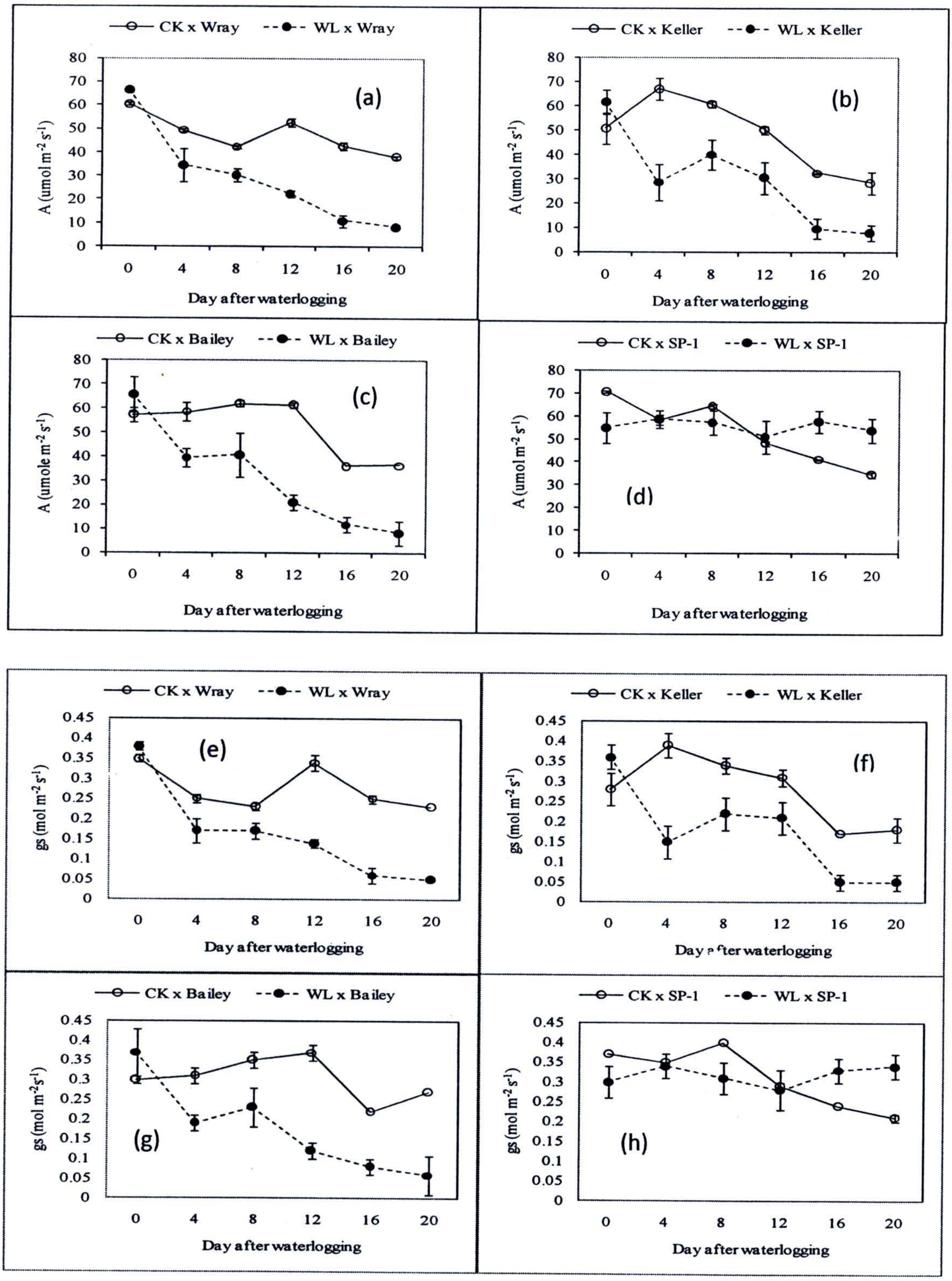

Figure 4 Effect of waterlogging on photosynthetic rate (A) (a, b, c, and d) and stomatal conductance (gs) (e, f, g, and h) of 4 sorghum cultivars. Solid lines and open symbols represent control plants, broken lines and closed symbols represent waterlogged plants. Error bars represent standard errors.

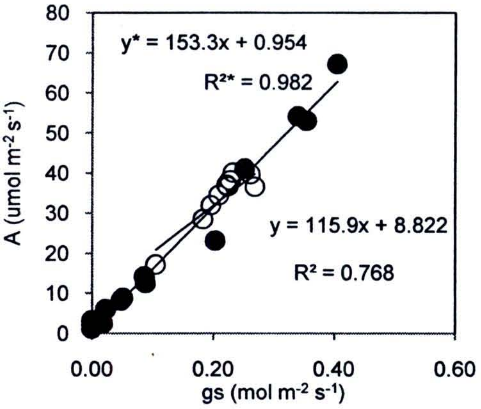

Figure 5 Relationships between photosynthetic rate (A) and stomatal conductance (gs) of sorghum. Open symbols represent control plants and filled symbols represent waterlogged plants. Asterisks represent responses in waterlogged plants.

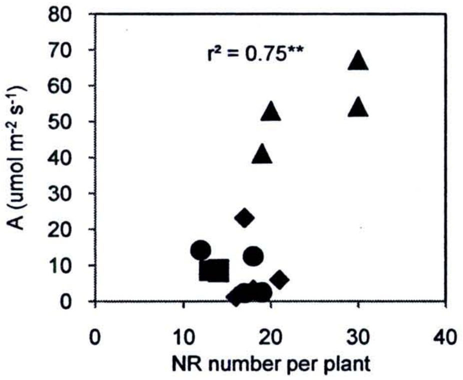

Figure 6 Relationships between nodal root (NR) number per plant and photosynthetic rate (A) under waterlogging conditions. Wray (■), Keller (●), Bailey (♦) and SP-1 (▲), n=16.